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THE LARVAL DEVELOPMENT OF NORTHERN CALIFORNIA *PORCELLANIDAE* (DECAPODA, ANOMURA). I. *PACHYCHELES PUBESCENS* HOLMES IN COMPARISON TO *PACHYCHELES RUDIS* STIMPSON[1]

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The zoeae of the *Porcellanidae* (Decapoda, Anomura) possess extremely long rostral and posterior spines making them unique and easily identified in the plankton. However within the family, differences between genera and species are subtle and there is a growing interest in culturing the zoeae from hatching to determine taxonomically important characteristics. At present, larval descriptions for twenty species in seven genera are available. These are as follows:

Porcellana
- *P. platycheles* (Lebour, 1943; LeRoux, 1961)
- *P. bluteli* (Bourdillon-Casanova, 1956)
- *P. longicornis* (LeRoux, 1966)
- *P. ornata* (Sankolli, 1967)

Polyonyx
- *P. quadriungulatus* (Knight, 1966)
- *P. hendersoni* (Sankolli, 1967)
- *P. gibbesi* (Gore, 1968)

Pisidia
- *P. longicornis* (Lebour, 1943)
- *P. spinulifrons* (Sankolli, 1967)

Petrolisthes
- *P. armatus* (Lebour, 1943, 1950; Gore, 1970)
- *P. rufescens* (Gohar and Al-Kholy, 1957)
- *P. elongatus* (Greenwood, 1965)
- *P. novaezelandiae* (Greenwood, 1965)
- *P. lamarckii* (Sankolli, 1967)

Pachycheles
- *P. rudis* (Knight, 1966)
- *P. haigae* (Boschi, Scelzo and Goldstein, 1967)
- *P. natalensis* (Sankolli, 1967)

Euceramus
- *E. praelongus* (Roberts, 1968)

Megalobrachium
- *M. poeyi* (Gore, 1971)

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Two species of *Pachycheles*, *P. pubescens* Holmes and *P. rudis*, are found on the California coast north of San Francisco. The adults are distinguished on the basis of the shape of the carpus and carapace, by the hairiness of the chela, and by the number of telson plates on the female (Haig, 1960). Both species have been collected in rocky intertidal regions from British Columbia to Baja California.

As noted above, Knight (1966) cultured and described the zoeae of *P. rudis*. The present paper presents a description of the larval development of *P. pubescens*. Because of the similarity of the two species, *P. rudis* was cultured along with *P. pubescens*. *Pachycheles rudis* zoeae were found to be identical to Knight's (1966) description. A subsequent paper will contain larval descriptions of the genus *Petrolisthes*, which is the only other genus of *Porcellanidae* on the northern California coast, and it should then be possible to identify *Porcellanidae* zoeae collected from this area to the species level.

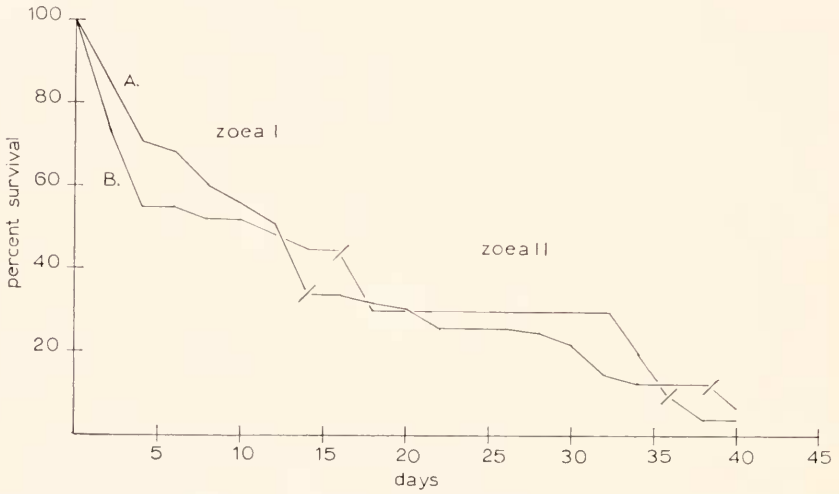

FIGURE 1. The per cent survival of *Pachycheles pubescens* Holmes plotted at two day intervals for the duration of its pelagic life. One hundred per cent represents 68 zoea in series A, 20 zoea in series B.

MATERIALS AND METHODS

The larvae of *P. pubescens* were found to be almost identical to those of *P. rudis* at hatching and it was necessary to culture series of zoea of both species simultaneously. To further substantiate the results, series of zoea were cultured from two females of each species.

Three ovigerous females of *Pachycheles pubescens* and two of *Pachycheles rudis* were collected during −1.0 tides on the north jetty, Doran Park, Sonoma County, California, in October, January and February, 1970–1971. The adults were maintained separately in plastic aquaria on sea water tables until the zoea hatched.

Zoeae were transferred to 62 mm stender dishes containing approximately 25 cc of filtered sea water. Two zoeae were cultured per dish. The dishes were

covered and placed in a dark refrigerator at 14° C ± 1° C. Salinity ranged from 30.0‰ to 34.0‰. During the period of the experiment the temperature and salinity of the ocean were monitored. Ocean temperature ranged from 9 to 14° C; salinity ranged from 32.0 to 36.0‰.

TABLE I

Measurements (mm) of the carapace, rostrum, posterior spine and rostrum/posterior spine ratio in the zoea of Pachycheles pubescens *and* P. rudis

	carapace	rostrum	p. spine	ros./p. spine
Zoea I				
P. pubescens (ser. A)				
mean	1.48	5.18	2.52	2.10
range	1.38–1.63	4.85–5.63	2.25–2.75	1.87–2.25
no. examined	15	15	15	15
P. pubescens (ser. B)				
mean	1.56	5.42	2.50	2.19
range	1.50–1.63	4.63–5.75	2.38–2.63	1.82–2.70
no. examined	15	15	15	15
P. rudis				
mean	1.49	5.33	2.80	1.93
range	1.38–1.60	5.00–5.75	2.38–3.00	1.75–2.34
no. examined	20	19	19	18
P. rudis (Knight, 1966)				
mean	—	5.78	3.00	—
range	—	5.64–5.92	2.92–3.08	—
no. examined	—	15	17	—
Zoea II				
P. pubescens				
mean	2.28	6.92	2.84	2.45
range	2.18–2.38	6.13–7.75	2.50–3.40	2.13–2.64
no. examined	6	6	6	6
P. rudis (Knight, 1966)				
mean	—	8.39	3.69	—
range	—	8.00–9.08	3.48–3.88	—
no. examined	—	7	6	—

Every second day the zoeae were transferred with a large bore plastic pipette into dishes containing fresh filtered sea water at 14° C. At this time a drop of concentrated culture of newly hatched *Artemia salina* (L.) nauplii was added as food, and the number of deaths and molts were counted.

Measurements of the whole zoeae, accurate to 0.05 mm, were made under a stereo-microscope with an ocular micrometer. Carapace measurements were made from the base of the rostrum to the base of the posterior spines. Only intact rostra and posterior spines were measured. Specimens of each developmental stage and exuvia were preserved in ethylene glycol.

Propylene phenoxetol was used as a narcotizing agent. Specimens of each stage of each species were dissected and the appendages examined under bright field illumination on a Leitz OrthoLux compound microscope. Drawings and measurements of the appendages were made with the aid of a camera lucida.

Results

Ovigerous females of *Pachycheles pubescens* were kept as long as 49 days before the eggs hatched. The females, with carapace widths from 10.0 to 12.5 mm, produced 25, 68 and 107 zoeae. The first zoeal stage lasted from 8 to 16 days and from 34 to 45 per cent survived to the second stage. The total pelagic larval phase extended from 34 to 40 days and there was only a 4 to 5 per cent

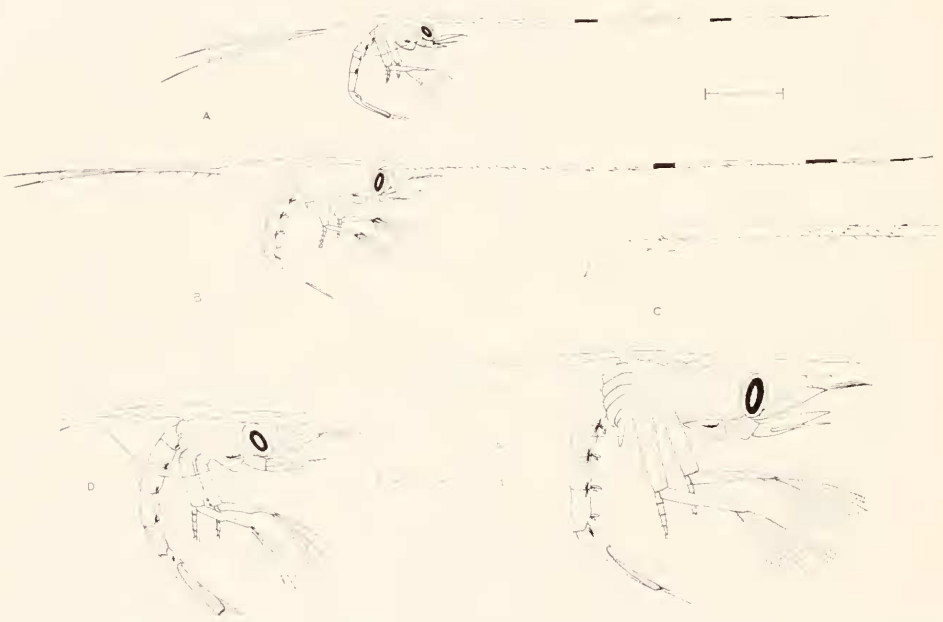

Figure 2. The zoeal stages of *Pachycheles pubescens* Holmes: A, D, first zoea; B, E, second zoea; C, setation of rostrum. Scale lines equal 1.0 mm.

survival to glaucothoe. In Figure 1, the per cent survival of the first and second zoeal stages is graphed for every 48 hour period. In both series there was a high mortality in the first zoeal stage, particularly during the first four days after hatching. A second high mortality occurred before the glaucothöe; in fact, a number of zoeae actually died in the process of molting to this stage. These two periods seem to be the most critical in the larval development. It is probable that there are critical temperature, salinity or other physiological requirements at this time (Costlow, Bookhout and Monroe, 1960).

Measurements of the carapace, rostrum, posterior spines and ratio of the rostral to the posterior spines for the two zoeal stages of *P. pubescens* and *P. rudis* are presented in Table I. There is no significant difference in size between the

first zoeal stages of the two species. However, in Knight's (1966) culturing of *P. rudis,* the rostrum and posterior spines of the second zoeal stage were longer than those of *P. pubescens.* Knight also reported that larger specimens of *P. rudis* were collected in the plankton. It is probable that size is variable and in part determined by one or more environmental factors.

Description

The carapace, abdomen and appendages of each stage are described with respect to setation and, in some cases, to relative size. Plumose and non-plumose setae have not been differentiated in the text; the reader is asked to refer to the illustrations for these details.

Zoea I

Carapace (Fig. 2A). The carapace is shallow, inflated and produced into a long rostrum and two posterior spines. The rostrum bears spinules which are concentrated on the ventral surface. The spinules completely encircle the rostrum only in the mid region of the length (Fig. 2C). The posterior spines bear a single row of 14 or 15 ventral spines.

Antennule (Fig. 3A). The unsegmented antennule bears six terminal processes: 3 aesthetes, 2 plumose setae, and one hair.

Antenna (Fig. 3B). The endopodite is fused to the protopodite and has a small hair on the inner margin. The exopodite is a movable spine which is almost 2 times as long as the endopodite and nine times as long as it is wide. It is armed with 3, or occasionally 4, curved hooks on the inner margin. On the intact animal the antenna is slightly shorter than the antennule.

Mandibles (Fig. 3C). The mandibles are asymetrical with small teeth and molar processes. Palps are absent.

Maxillule (Fig. 3D). The endopodite is unsegmented and bears 3 terminal setae and a single strong subterminal seta. There is a row of setules on the outer border. The basal endite has teeth and three setae; the coxal endite has 9 long curved processes.

Maxilla (Fig. 3E). The scaphognathite bears 6 setae along the lateral margin and a single long seta on the apex. Setules are present between the setae. The endopodite has 6 terminal and 2 subterminal setae and setules along the outer border. The basal endite has 7–8 processes on the distal lobe and 6–7 on the proximal lobe. The coxal endite bears 4 processes on the distal lobe and 8 on the proximal lobe.

First maxilliped (Fig. 3F). Two setae are present on the inner margin of the coxopodite. The basipodite has 10 setae along the margin in groups of 2, 2, 3 and 3 progressing distally. The endopodite is four segmented. The distal segment bears 9 terminal setae and 1 long plumose subterminal seta. The third segment has 3 distal setae and 1 medial seta; the first and second segments each have 3 setae. There are no setules on the outer margin of the endopodite. The exopodite is indistinctly 2 segmented and ends with 4 natatory setae.

Second maxilliped (Fig. 3G). The coxopodite is unarmed. The basipodite has 3 setae in groups of 1 and 2 progressing distally. The endopodite is four

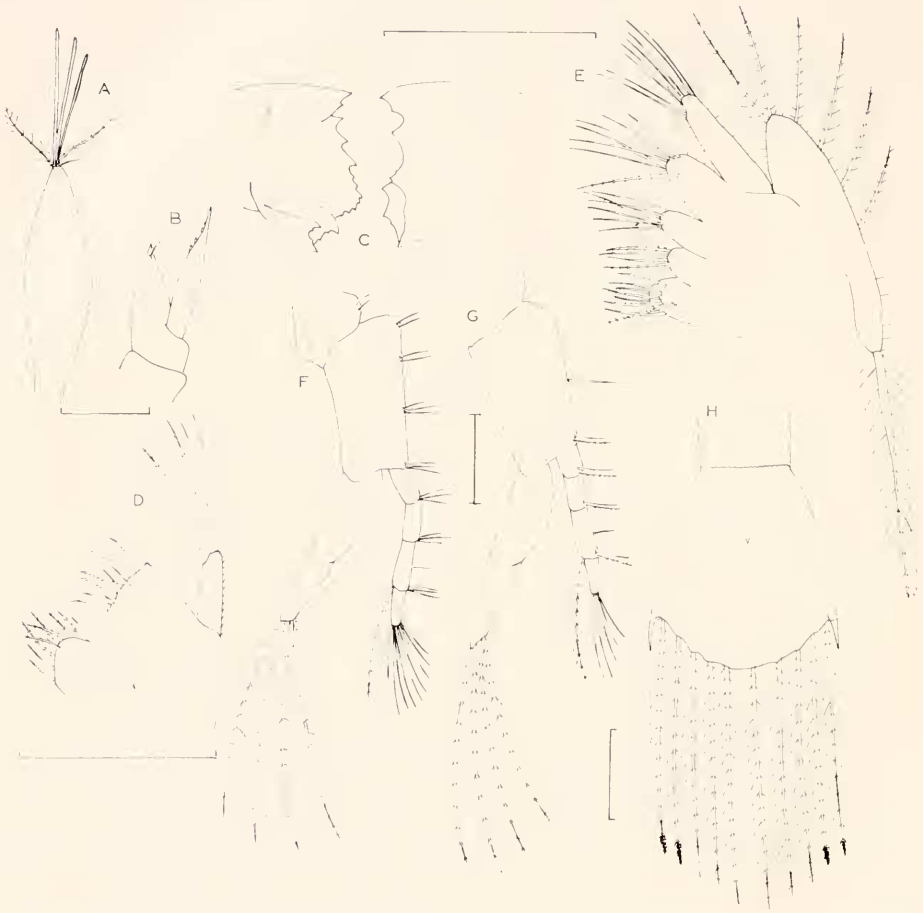

FIGURE 3. *Pachycheles pubescens* Holmes: first zoeal appendages; A, antennule; B, antenna; C, mandibles; D, maxillule; E, maxilla, F, first maxilliped; G, second maxilliped; H, third maxilliped; I, telson. Scale lines equal 0.2 mm.

segmented. The distal segment bears 5 terminal setae and 1 long subterminal seta. The third segment has 2 distal setae and 1 medial seta; the first and second segments each bear 2 setae. There are no setules on the inner margin of the endopodite. The exopodite is indistinctly 2 segmented and ends with four natatory setae.

Third maxilliped and periopods. The third maxilliped and periopods are rudimentary buds beneath the carapace.

Abdomen (Fig. 2D). The abdomen consists of five somites. Each somite has a row of fine teeth around the dorsal margin and somites 4 and 5 have small lateral spines.

Telson (Fig. 3H). The telson is as long as it is wide, and bears the standard $7 + 7$ terminal processes. The third and fourth processes (first and second

long spines) are each armed with curved hooks at the tips. An anal spine is present.

Coloration (Fig. 2D). A pair of red chromatophores is present around the mouth, on the abdominal somites 1 through 4 and on the telson. An orange-red

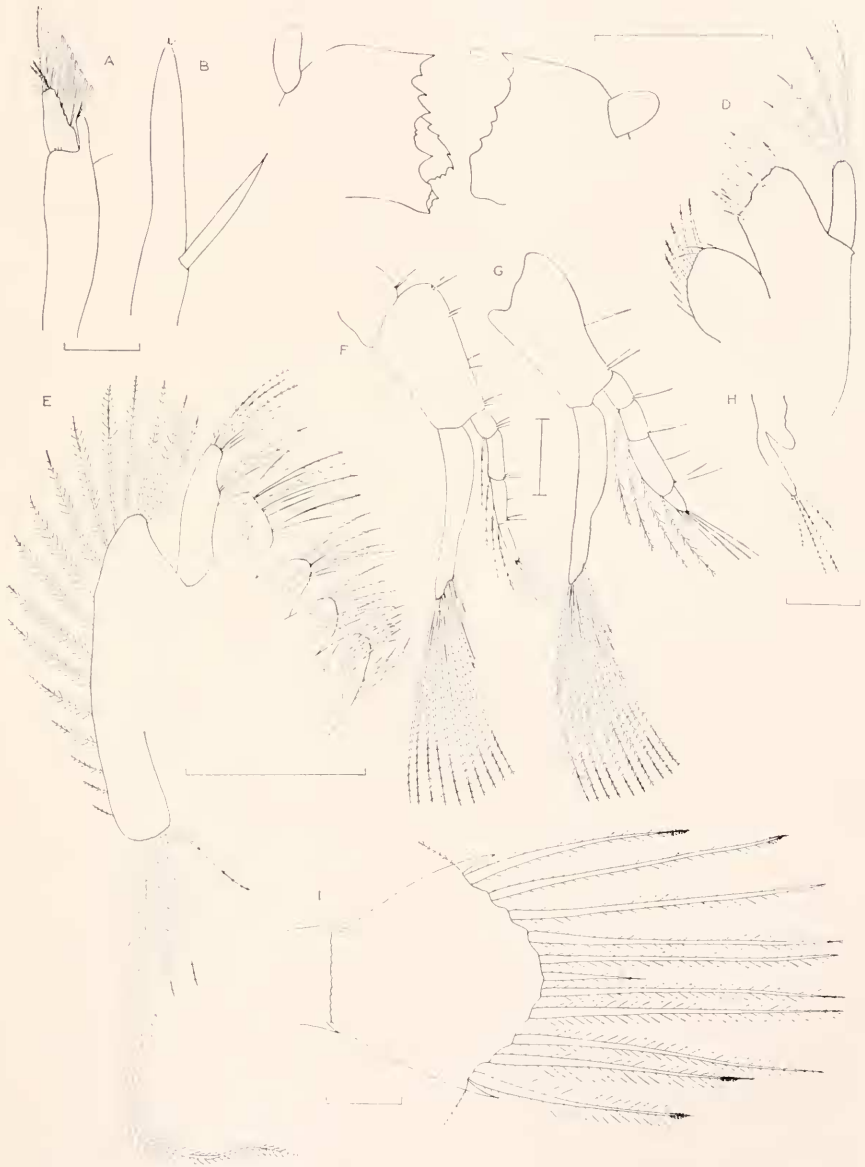

FIGURE 4. *Pachycheles pubescens* Holmes: second zoeal appendages; A, antennule; B, antenna; C, mandibles; D, maxillule; E, maxilla; F, first maxilliped; G, second maxilliped; H, third maxilliped; I, telson. Scale lines equal 0.2 mm.

coloration is apparent on the tips of the posterior spines and forms three bands around the rostrum.

Zoea II

The eyes are definitely stalked, the exopodites of the maxillipeds bear 12–14 natatory setae and pleopod buds are present on the abdominal somites.

Antennule (Fig. 4A). The antennule is biramous. The exopodite bears 7 terminal processes: 3 aesthetates, 1 long and 2 small plumose setae and a small hair. There are five tiers of aesthetates along the inner margin in groups of 4, 4, 2, 2 and 2 progressing distally. The endopodite is unarmed and fused to the protopodite. The protopodite bears a single seta on the distal corner.

FIGURE 5. *Pachycheles pubescens* Holmes: Glaucothöe and glaucothöe locomotory appendages; A, first pleopod; B, fourth pleopod; C, telson; D, cheliped; E, walking leg; F, fifth periopod. Scale lines equal 0.5 mm.

Antenna (Fig. 4B). The endopodite has greatly increased in relative length and terminates in a small tooth and a hair. The exopodite has lost the hooks on the inner margin.

Mandibles (Fig. 4C). The mandibles now possess a rudimentary palp.

Maxillule (Fig. 4D). The endopodite is unchanged. The basal endite bears 5 long curved spines and 6 setae.

Maxilla (Fig. 4E). The scaphognathite has 16–18 setae around the lateral margin. In addition there are 4 apical setae of which the outermost is by far the longest. The endopodite has 6 terminal and 3 subterminal setae. The basal endite bears 10 processes on the distal lobe and 9–10 on the proximal lobe; the coxal endite has 6–7 on the distal lobe and 10–12 on the proximal lobe.

First maxilliped (Fig. 4F). The exopodite now terminates in 14 natatory setae. On the endopodite, segments 1 through 4 each have an additional long seta on the outer margin. The terminal segment ends in 10 setae.

Second maxilliped (Fig. 4G). The exopodite now terminates in 12 natatory setae. The first three segments of the endopodite have an additional long seta on the outer margin. The third segment is swollen.

Third maxilliped (Fig. 4H). The endopodite is rudimentary and consists of a swollen bud. The exopodite bears four terminal setae.

Periopods. The peripods have increased in size beneath the carapace.

Pleopods. Pleopod buds are present on abdominal somites 2, 3, 4 and 5.

Telson (Fig. 4I). The telson has an additional spine on the central prominence.

Glaucothöe

Carapace (Fig. 5). The carapace is sharply serrated on the anterior margin and dentate along the lateral margins. Length × width: 1.5 × 1.4 mm.

Antennule (Fig. 6A). The antennule is biramous. The peduncle is three segmented; the basal segment is enlarged and dentate. The outer ramus is five segmented and bears a row of long aesthetates on the inner border. The lower ramus is three segmented with a group of long setae on the distal margin of the proximal segment. Other setae are placed as illustrated.

Antenna (Fig. 6B). The peduncle is three segmented. The proximal segment has a blade-like extension on the outer margin. The flagellum consists of about 25 segments each with several short setae on the anterior margin.

Mandibles (Fig. 6C). The teeth have been reduced; the palp is three segmented with 10 short spines on the terminal segment.

Maxillule (Fig. 6D). The endopodite is unsegmented and bears 4 setae. The basal endite has about 15 teeth and 9 setae; the coxal endite has about 30 spines.

Maxilla (Fig. 6E). The scaphognathite is fringed with 51 setae. The endopodite is unsegmented and has 2 long setae. The basal endite is armed with about 27 processes on the distal lobe and about 16 on the proximal lobe. The distal lobe of the coxal endite bears about 10 terminal setae and 10 subterminal setae. The proximal lobe bears 15 subterminal and 19 terminal setae.

First maxilliped (Fig. 6F). The exopodite and endopodite are reduced and unsegmented. The exopodite has 6 setae along the outer margin. The protopodite bears about 40 processes on the basal lobe and 11 on the coxal lobe.

Second maxilliped (Fig. 6G). The exopodite is two segmented. The distal segment has 6 terminal and 4 subterminal setae. The proximal segment has 4 or 5 setae. The endopodite is four segmented. Progressing proximally these segments are armed with about 18, 15, 5 and 7 setae. The basipodite has 9 setae on the outer margin and 1 on the inner margin. The coxopodite has 6 setae on the outer margin.

Third maxilliped (Fig. 6H). The exopodite is unsegmented and devoid of setae. The endopodite consists of 5 segments. The distal segment bears 7 long setae. The outer borders of the next three segments each are lined with from 7 to 13 setae. The fourth segment from the tip is armed with a toothed blade-like extension. The most proximal segment has 9 setae on the outer border.

Periopods (Fig. 5D, E, F). The subequal chelipeds are serrate along the edges and sparsely covered with tubercles and setae. The carpus has two large teeth on the inner margin (Fig. 5D). The walking legs are covered with long setae which are most dense on the ventral margin. The dactyls have 3 spines

FIGURE 6. *Pachycheles pubescens* Holmes: Glaucothoe sensory and feeding appendages; A, antennule; B, antenna; C, mandible; D, maxillule; E, maxilla; F, first maxilliped; G, second maxilliped; H, third maxilliped. Scale lines equal 0.2 mm.

on the inner margin. The propodus has 2 spines on the anterior dorsal corner and 2 more on the dorsal margin (Fig. 5E). The fifth periopod is chelate. The chelae are armed with from 4 to 6 scythe-like hooks and numerous setae (Fig. 5F).

Pleopods (Fig. 5A, B). There are four pair of Pleopods which decrease in size from the second to the fifth somite. The setation is variable. The exopodites

TABLE II

Summary of distinguishing morphological characteristics of Pachycheles pubescens, P. rudis (*Knight, 1966*), P. haigae (*Boschi et al., 1967*) and P. natalensis (*Sankolli, 1967*)

	P. pubescens	*P. rudis*	*P. haigae*	*P. natalensis*
Zoea I				
Antenna				
exopodite, no. hooks	3–4	3	4	3
Maxillule				
basal endite, no. setae	9	9	9	8
Maxilla				
scaphognathite, no. setae	6	6	6	7
endopodite, no. setae	12	12	12	8–9
First maxilliped				
basipodite, no. setae	9	9	9	10
endopodite				
4th segment, no. setae	9–10	7–8	10	8
3rd segment, no. setae	3 + 1	3 + 2	4 + 3	6
2nd segment, no. setae	3	3	2	4
1st segment, no. setae	2	2	3	2
Second maxilliped				
endopodite				
4th segment, no. setae	5	5	7	5
3rd segment, no. setae	3	3	2	3
1st & 2nd segments, no. setae	2	2	3	2
Telson, no. spines with hooks	4	4	4	10
Zoea II				
Mandibles, palps	+	+	0	—
Maxilla				
scaphognathite, no. lateral setae	17–18	20–22	18	—
First maxilliped				
endopodite				
inner margin, no. setae	4	3	4	—
4th segment, no. setae	10	8	10–12	—
Second maxilliped				
endopodite, no. setae on inner margin	4	3	4	—
Third maxilliped, no. setae	4	2	2	—

have from 10 to 13 setae. The endopodites have from 2 to 4 small hooks and a single seta.

Telson (Fig. 5C). The telson is a semicircular plate with a distinct medial notch. The posterior border has 17 long setae and 14 shorter setae. Hooks

characteristic of the zoeal telson setae are not present in the glaucothöe. The ventral surface is sparsely covered with short setae. The uropods have 14 setae on the exopodite and 11 setae on the endopodite. There are also 5 short setae on the outer border of the endopodite.

Coloration (Fig. 5). Red chromatophores are distributed on the carapace, eyestalks, periopods and mouth parts. Four large red chromatophores are present between the abdominal segments.

Discussion

The zoeae of *P. pubescens* are very similar to those of *P. rudis*. The first zoeal stages can be distinguished only by the setation of the endopodite of the first maxillipeds. In *P. pubescens*, the fourth segment has 9 or 10 setae and the third segment has 1 medial seta. In *P. rudis* there are only 7 or 8 terminal setae on the fourth segment and 2 medial setae on the third (Table II). The species diverge in the second stage. In addition to the differences listed above, there are four long setae on the inner margin of the endopodite of the first and second maxillipeds in *P. pubescens* and only three in *P. rudis*. *P. pubescens* has four setae on the exopodite of the third maxilliped; *P. rudis* has only two. The scaphognathite of the maxilla also differs. In *P. pubescens* there are 17–18 setae along the lateral margins; in *P. rudis* there are 20–22.

The two California species have more in common with each other than they do with other described species. Because the zoeae of the two species are so similar, Knight's (1966) comparison of *P. rudis* zoeae collected from the plankton with those cultured in the laboratory is questionable.

Knight (1966) did not describe the appendages of the *P. rudis* glaucothöe. Only one specimen was obtained from the present culturing of that species which was in poor condition. It was evident however that the carpus, which is an important taxonomic characteristic in the adult, can be used to distinguish the glaucothöe of the two species. The anterior margin of the carpus is produced into two large spines in *P. pubescens* and only one in *P. rudis*.

The zoea of the northern California species differ from *P. haigae* (Boschi *et al.*, 1967) in the number of hooks on the antennal exopodite and in the setation of the second maxilliped in the first stage, and in the lack of palps on the mandibles in the second stage. In addition, the Indian species, *P. natalensis* (Sankolli, 1967), differs in the setation of the maxillule and maxilla and in the number of telson spines with hooks at the tips (Table II).

The chromatophore distribution is identical in *P. pubescens* and *P. natalensis* (Sankolli, 1967). The descriptions of *P. rudis* (Knight, 1966) and *P. haigae* (Boschi *et al.*, 1967) do not include notes on coloration. However *P. rudis* cultured at this laboratory was found to have the same pattern of chromatophore distribution as *P. pubescens* and *P. natalensis*. This color pattern may prove to be characteristic of the genus, but at this point too few species have been described to make any generalizations. Other characteristics which may prove peculiar to the genus, particularly in differentiating it from *Petrolisthes*, may be the lack of setules on the endopodites of the first and second maxillipeds in zoea I and the two outermost pair of telson spines only with hooks on the tips (although *P. natalensis* differs in the second respect).

In conclusion, *Pachycheles pubescens* and *Pachycheles rudis* are almost identical at hatching and diverge later in development. The two species seem to be more closely related to each other than they are to other described species. The first maxilliped is the most variable feature between species within the genus. Chromatophore distribution, number of telson spines tipped with hooks, and the absence of setules on the inner margin of the endopodites of the maxillipeds may prove to be important characteristics of the genus.

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Summary

Two species of *Pachycheles* (Decapoda, Porcellanidae) occur along the northern California coast: *P. pubescens* and *P. rudis*. The zoeae of the two species are very similar. At hatching they differ only in the setation of the first maxilliped, however they diverge later in development. The setation of the first maxilliped appears to be the most variable feature of species of this genus so far described. Chromatophore distribution, number of telson spines with hooks at the tip, and the absence of setules on the inner margin of the endopodites of the maxillipeds may prove to be important in differentiating *Pachycheles* from other *Porcellanidae*, particularly from the genus *Petrolisthes*.

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